

REVISIONARY STUDY OF THE GENUS *MILLERIA* (ASTERACEAE,
HELIANTHEAE)

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ABSTRACT

The genus *Milleria* is treated as having two species, a widespread tropical or subtropical weedy annual, *M. quinqueflora*, (including the recently described *M. peruviana* H. Rob) and *M. perfoliata* B.L. Turner, *spec. nov.*, which is proposed to accommodate a single collection from El Tuito, Jalisco, having features markedly different from those of *M. quinqueflora*, with which it grows. These include: glabrous stems, smaller, markedly perfoliate leaves, smaller heads with more numerous (6-8 vs. 4) yellow (vs. green), disk florets, and yellow anthers (vs. purplish-black). Detailed distributional maps are provided.

KEY WORDS: Asteraceae, *Milleria*, Heliantheae, systematics

Milleria, a very distinct genus containing only one or two annual herbs, was first proposed by Linnaeus in 1735 and formally established by him in the first edition of his *Species Plantarum*. As originally proposed it was thought to comprise two species, *M. quinqueflora* L. and *M. biflora* L., but the latter was subsequently removed and given generic status as *Delilia* (cf., Delprete 1995).

Most recent workers have treated *Milleria* as monotypic, but H. Robinson (1981) proposed an additional species, *M. peruviana* H. Rob., at the time thought to be confined to Perú. We have reduced the latter to synonymy with *M. quinqueflora* but the senior author has felt compelled to propose yet another taxon for the genus, *M. perfoliata* B.L. Turner, from a single bizarre collection made in Jalisco, México, where it co-occurs with *M. quinqueflora*.

CHROMOSOMES

Powell & Turner (1963) were the first workers to report chromosome numbers for *Milleria*, noting *M. quinqueflora* to possess fifteen bivalents at Meiosis I, these appropriately illustrated. Subsequent workers (Turner & King 1964; Keil, *et al.* 1988) have confirmed this number, as indicated in the following list:

MEXICO: Jalisco, *Powell 845* (TEX), Powell & Turner (1963)

MEXICO: Michoacán, *Keil 15145A* (OBI), Keil, *et al.* (1988)

PANAMA: Cocle, *King 5324* (TEX), Turner & King (1964)

PANAMA: Panamá, *King 5461* (TEX), Turner & King (1964)

The above four counts, all diploid ($2n=30$), were obtained from meiotic configurations. This suggests a base number of $x=15$, if not $x=10$, for *Milleria*. Closely related genera on a base of $x=15$ include *Trigonospermum*, *Guizotia*, *Polymnia*, *Smallanthus*, and *Sigesbeckia*, although the latter also contains diploid species with $2n=20$, suggesting that the ancestral base number for the complex might be $x=10$.

GENERIC RELATIONSHIPS

Bentham & Hooker (*Gen. Plant.* 2:190. 1873.) were the first to propose the subtribe Milleriinae with any rigor, albeit artificially circumscribed, recognizing in this sixteen genera. Hoffmann in his treatment of the Compositae for the *Natürlichen Pflanzenfamilien* largely followed the work of Bentham & Hooker. Before this time, however, Cassini recognized a milleroid generic grouping, which included many of the genera so treated by subsequent workers.

Stuessy (1977) noted that it was difficult to assess relationships of the milleroid genera because of the high degree of reduction found in their floral parts. He largely accepted the subtribe as constituted by Bentham, but recognized in this three groups:

GROUP 1 (Herbs with solitary or few heads having 1 ray floret). *Koehneola*, *Milleria*, *Pinillosia*, *Sheareria*, *Tetranthus*, and *Tetraperone*

GROUP 2 (Herbs with heads tightly clustered each having 1 ray floret). *Delilia*, *Lantanopsis*, and *Riencourtia*

GROUP 3 (shrubs with heads in few-to-many clusters; ray florets 3-many). *Clibadium*, *Desmanthodium*, *Ichthyothere*, and *Stachycephalum*

Robinson (1981) drastically revised the subtribe Milleriinae, transferring out of this *Sheareria* (to the tribe Astereae); *Delilia* and *Tetranthus* (to the subtribe Ecliptinae, a large "grab bag" group with 64 or more genera); *Ichthyothere* (to the subtribe Melampodinae); *Clibadium*, *Lantanopsis*, and *Riencourtia* (to the subtribe Clibadiinae); *Desmanthodium* and *Stachycephalum* (to the subtribe Desmanthodiinae); and *Pinillosia* (to the subtribe Pinillosinae).

Robinson retained *Milleria* in his newly conceived subtribe Milleriinae which contained, in addition (listing these alphabetically): *Axiniphyllum*, *Guizotia*, *Rumfordia*, *Sigesbeckia*, and *Trigonospermum*. He reckoned, however, that *Milleria*

showed "relationships to a group of genera including *Rumfordia*," all of these recognized by a syndrome of features, the most notable being the relatively large, terete to trigonous, distinctly striate, carbonized achenal walls.

We largely agree with Robinson's assessment of the subtribe and believe this to be a much more natural grouping than proposed by previous workers. Indeed, we suggest that *Milleria* is perhaps most closely related to *Trigonospermum*, the latter often confused with *Milleria* by field collectors, and both possessing base numbers of $x=15$ (Robinson, *et al.* 1981), as do *Guizotia* and *Sigesbeckia* of this subtribe.

Finally, it should be noted that Karis & Ryding (1994) positioned *Milleria* in their broadly circumscribed subtribe Melampodinae, which included an array of 23 genera. Their morphological cladistic analysis of the tribe Heliantheae nested *Milleria* between a clade housing *Polymnia* and one housing *Melanpodium*, *Smallanthus*, and *Rumfordia*.

We do not pretend to have any deep insight into the phyletic relationships of *Milleria* except that the suggestions of Robinson (1981) and Karis & Ryding (1994) are perhaps better than most earlier reckonings. The senior author favors a close relationship of *Milleria* with *Trigonospermum*, but the latter genus, while included in the Melampodinae by Karis & Ryding, was not treated in their cladistic analysis.

Any certainty regarding the phyletic relationships of *Milleria* and closely related genera will certainly require DNA analysis, using both chloroplast and nuclear genes. Until then it's anybody's best guess, depending upon the characters emphasized and, in the case of cladistic analysis, selection of outgroups for character polarization.

TAXONOMY

MILLERIA L.

Annual herbs. Leaves opposite, simple, petiolate or perfoliate; blades 3-nervate from the base. Heads numerous, arranged in terminal cymose panicles. Involucre small; bracts 2-seriate, subequal, thin and scarious at first, at maturity becoming ligneous and tightly investing the achenes. Ray florets pistillate, fertile, 1 or rarely 2; ligules small, yellow, 3-lobed. Disk florets perfect but functionally staminate, sterile; corollas green or bright yellow; anthers purplish-black or yellow. Base chromosome number, $x=15$.

KEY TO SPECIES

1. Leaves markedly perfoliate, the blades lanceolate, 1.5-2.0 cm wide; ultimate peduncles 10-20 mm long; staminate florets 6-8, the corollas yellow; anthers yellow; near El Tuito, Jalisco, México. *M. perfoliata*

1. Leaves not clearly perfoliate, the blades broadly ovate and tapering into well-defined petioles, those at midstems mostly 3-10 cm wide; ultimate peduncles ca. 5 mm long; staminate florets 4, rarely 5, the corollas greenish; anthers purplish-black; widespread weed in tropical and subtropical regions of the New World.
.....*M. quinqueflora*

MILLERIA QUINQUEFLORA L., *Sp. Pl.* 919. 1753. TYPE: According to Stuessy (1977), type material of this species was obtained from material cultivated in the Uppsala Botanical Garden; the source of seed and collector unknown. He notes the "holotype" to be in the Linnean Herbarium 1031.1 (*cf.*, IDC 177.621:1.1). Actually, at least two sheets of *M. quinqueflora* are on file in the Linnean Herbarium (catalogue numbers 1031.1 and 1031.2, the former having the name "quinqueflora" written on the sheet itself, presumably by Linnaeus). It is likely that the seeds from which type material was grown came from Mr. Philip Miller (for which the genus was named), gardener at the Botanical Gardens at Chelsea, England, who apparently obtained the original seeds from a Mr. R. Millar, who collected these in "Campeachy," México (from the present seaport of Campeche, Yucatán Peninsula, México), which Millar visited in 1734 (*cf.*, below). The senior author has examined a sheet of *Milleria quinqueflora* (BM!) which has written on the reverse side, presumably in Linnaeus' own hand "This tribe of plants takes their name from that ingenuous Botanist Mr. Philip Miller who is gardner to W. Apothecary, at the Botanical Garden at Chelsea 1749." Below the plant is written "*Milleria foliis cordatis, pedunculis dichotomis. Hort. cliff. 425,*" the same description given in its protologue by Linnaeus.

Miller (*Gard. Dict.*, ed. 8. 1768.) provided additional clues as to the possible source of the Uppsala seeds. In his description of a new taxon *Milleria maculata* Mill., noted that this "... second set was discovered by Mr. Robert Millar, at Campeachy [Mexico], in the year 1734; this approaches near to the first sort [*M. quinqueflora* typicus], but the stalks rise six or seven feet high, branching out very wide".

Miller then goes on to describe an additional "sort" (*Milleria triflora* Mill.) which was also discovered "by the late Mr. Robert Millar, at Campeachy; this is an annual plant, which rises with an upright stalk three or four feet high, garnished the whole length with oval spear-shaped leaves near four inches long . . . This flowers and seeds later in the year than either of the former, so that unless the plants are brought forward in the spring, they will not ripen their seeds in England." We surmise, considering the above, that Linnaeus received his original garden seed from Philip Miller, who had presumably grown the plant over a number of years from the "Campeachy" seeds first collected by R. Millar in 1734. This has been dwelt upon here at some length to point out, not only the origin of the name, and something of its history, but also to emphasize how extremely variable *M. quinqueflora* can be, even from seeds obtained from a single source.

Milleria maculata Mill., *Gard. Dict.*, ed. 8. 1768. TYPE: Grown from seeds obtained in MEXICO. Campeche: Campeche, 1734, R. Millar s.n. *Milleria quinqueflora* L. var. *maculata* (Mill.) DC., *Prodr.* 5:503. 1836. (HOLOTYPE: BM, not examined).

Milleria triflora Mill., *Gard. Dict.*, ed. 8. 1768. TYPE: Grown from seeds obtained in MEXICO. Campeche: Campeche, 1734, *R. Millar s.n.* (HOLOTYPE: BM, not examined).

From the rather detailed description, both of the above names surely apply to *Milleria quinqueflora*, the former said to be a markedly serrate form of the latter, even by DeCandolle, who gave it varietal ranking.

Milleria glandulosa DC., *Prodr.* 5:503. 1836. TYPE: MEXICO. Morelos: Cuernavaca, 20 Oct 1827, *Berlandier* 955 (HOLOTYPE: G-DC; Photoholotypes: F!,MO!).

Milleria peruviana H. Rob., *Wrightia* 6:47. 1979. TYPE: PERU. Lambayeque: El Molino, a 20 km del cruce entre Olmos y Abra de Porculla, 700-800 m, 20 Apr 1953, *Ferreira* 9140 (HOLOTYPE: US!; Photoholotypes: F!,GH!,MO!,NY!,TEX!).

Erect tap-rooted herbs 0.3-1.5(-2.5) m high, stems fistulose, terete, variously glandular pubescent. Midstem leaves broad and thin, the blades 3-nerved from the base, broadly ovate to ovate-elliptic, mostly 6-15(-25) cm long, 3-14(-18) cm wide, grading into a well-defined petiole, sparsely scabrous above and below with broad-based hairs, the margins subentire to serrate dentate. Heads numerous, arranged in corymbose panicles, the ultimate peduncles glandular pubescent, 0.5-1.0 cm long. Involucres mostly 3-4 mm high, 4-6 mm across, the bracts mostly acute to obtuse, usually ciliate or pilosulous. Ray florets pistillate, fertile, yellow, 3-lobed, ligules 3-5 mm long. Disk florets 4(-5), sterile, the ovaries glabrous; corollas green or greenish. Anthers purplish-black. Achenes (including the encasing involucre) mostly irregularly ovoid, 4-5 mm across. Chromosome number, $2n=30$.

This species has been described in considerable detail by Nash (1976), Stuessy (1975), and McVaugh (1974), and all of these authors have provided excellent detailed line drawings of the species, thus it seems superfluous to add yet another, as construed in the above, albeit based upon more numerous sheets. Indeed, were it not for *Milleria perfoliata* proposed by the senior author in the present paper, we would have been content to state that *M. quinqueflora* is a robust annual weed with opposite leaves and small heads, each of the latter having a single yellow pistillate fertile ray floret and 4-5 sterile staminate florets, at maturity, the single black striate achene becoming tightly encased in a pea-sized structure formed by the enclosing highly modified involucre bracts.

Milleria triflora was inadvertently listed as *M. trifolia* Mill. in *Index Kewensis* (1st edition). From the original description, this plant is certainly a peculiar small-flowered, odd-leaved, form of *M. quinqueflora*, surely derived from a seed source of the latter, to judge from Miller's protologue, as noted in the above. It is possible that bizarre offspring from *M. quinqueflora* occur upon occasion, and such might account for the strikingly different *M. perfoliata*, described below.

Milleria glandulosa "is ordinary *M. quinqueflora* L." as noted by Blake (1930) who examined type material of the taxon in the Prodrum Herbarium (G-DC).

Milleria peruviana is a form of the species with the uppermost leaves ovate and essentially sessile. Such forms occur sporadically over the range of the species. Robinson thought his new species to be "the first record for the genus in Peru," but as indicated in our cited specimens, *M. quinqueflora* had been collected earlier in

northernmost Perú by Ferreyra, relatively close to the type locality of *M. peruviana* (Figure 4). Robinson, by annotation, would also attribute *M. peruviana* to both Ecuador (*Bro. Elias* 248 [US]) and Colombia (*Harling & Andersson* 24794 [US]), but we take these to be rather typical specimens of *M. quinqueflora*.

DISTRIBUTION (Figure 1) AND ECOLOGY: Tropical or subtropical regions of the New World, especially North America, where it occurs as a weed in ditches and cultivated fields from near sea level up to 1,000 meters, but occasionally higher (reportedly up to ca. 1800 m).

REPRESENTATIVE SPECIMENS: MEXICO. Sonora: *Gentry* 1684 (F,MO,NY,TEX). Chihuahua: *Palmer* 176 (GH,NY). Sinaloa: *Reveal* 4036 (MO,NY,TEX). Nayarit: *Cronquist* 9598 (NY). Jalisco: *Fernández N.* 2594 (NY). Colima: *Sanders* 8508 (TEX). Michoacán: *Hinton, et al.* 12157 (GH,LL,NY). México: *Hinton, et al.* 1707 (NY). Morelos: *Seler* 4199 (GH). Veracruz: *Hernández* 648 (NY). Guerrero: *Palmer* 5 (F,GH,MO,NY). Oaxaca: *Anderson* 13193 (NY). Chiapas: *Breedlove* 28330 (LL,MO). Campeche: *Lundell* 855 (F,GH,MO,NY,TEX). Yucatán: *Gaumer* 949 (F,GH,MO,NY). Quintana Roo: *Darwin* 2385 (F,MO).

BELIZE. *Gentle* 844 (F,LL,MO,NY,TEX).

GUATEMALA. Amatlán: *Ruana* 1275 (F). Chimaltenango: *Martin J.* 1328 (F). Chiquimula: *Steyermark* 30313 (F). Izabal: *Standley* 24407 (GH,MO). Jalapa: *Standley* 76500 (F). Jutiapa: *Dunn* 23281 (NY,TEX). Petén: *Contreras* 328 (F,LL). Santa Rosa: *Heyde & Lux* 4110 (NY). Baja Verapaz: *Molina* 27809 (F). Zacapa: *Standley* 74779 (F).

EL SALVADOR. Ahuachapán: *Standley* 2765 (F). La Libertad: *Roweder* 3477 (MO). San Salvador: *Calderón* (F,GH,MO,NY). San Vicente: *Standley* 3580 (F). Sonsonate: *Standley* 22199 (GH,NY).

HONDURAS. Lempira: *Nelson* 283 (F,MO). Morazán: *Standley* 27485 (GH,MO). Olancho: *Standley* 17717 (F). Valle: *Zelaya* 231 (MO).

NICARAGUA. Boaca: *Seymour* 6085 (GH). Carazo: *Kral* 69380 (MO). Chinandega: *Baker* 2022 (GH,LL,NY). Chontales: *Stevens* 4070 (MO). Esteli: *Stevens* 15879 (MO). Granada: *Moreno* 9958 (F). Jinotega: *Croat* 42886 (MO). León: *Guzman* 10056 (MO). Madriz: *Stevens* 16150 (MO). Managua: *Neill* 7497 (GH,NY). Masaya: *Araguistan* 417 (TEX). Matagalpa: *Molina R.* 22850 (NY). Rivas: *Robledo* 1090 (F). Zelaya: *Bunting* 665 (NY).

COSTA RICA. Alajuela: *Brenes* 17240 (F,NY). Guanacaste: *Opler* 1835 (F,MO). Puntarenas: *Morrison* 8778 (GH). San José: *Weston* 1797 (F).

PANAMA. Canal Zone: *Woodson* 1420 (GH,NY). Chiriqui: *Woodson* 843 (GH). Cocle: *Dwyer* 1171 (F,GH,MO). Colón: *Dwyer* 4524 (MO). Herrera: *Croat* 4135 (MO). Panamá: *Woodson* 1545 (LL,NY). Veragua: *Dwyer* 4269 (MO).

COLOMBIA. Atlántico: *Elias* 248 (F,NY). Bolívar: *Killip* 14249 (F,GH,NY). Magdalena: *Hought* 3725 (F,NY).

ECUADOR. El Oro: *Asplund* 15767 (NY). Guayas: *Hitchcock* 20586 (GH,NY).

VENEZUELA. Aragua: *Fernández* 573 (F). Carabobo: *Pittier* 8947 (GH). Caracas: *Bailey* 796 (MO,NY). Cojedes: *Trujillo* 13921 (F). Lara: *Steyermark* 111058 (F). Merida: *Breteler* 3985 (F). Portuguesa: *Paez* 6 (MO). Tachira: *Bunting* 110 (NY). Valera: *Alston* 5289 (F). Yaracuy: *Croat* 54597 (F).

PERU. Tumbes: *Ferreyra* 5982 (F).



Milleria

Figure 1. Documented distribution of *Milleria quinqueflora* as determined from the specimens examined. Collections from near Havana, Cuba and the island of Trinidad, indicated by closed circles, probably represent relatively recent introductions.



Figure 2. Documented distribution of *Milleria quinqueflora* in México, Belize, and Guatemala.



Figure 3. Documented distribution of *Milleria quinqueflora* in Central America.



Figure 4. Documented distribution of *Milleria quinqueflora* in South America.

CUBA: *Bro. León 7321* (NBY).

TRINIDAD: *Broadway 5846* (LL).

MILLERIA PERFOLIATA B.L. Turner, *spec. nov.* TYPE: MEXICO. Jalisco: El Tuito, "a 8-3 km por el camino El Tuito-Ixtlahuahuey. Bosque de Pino-encino, en vegetación secundaria cerca de un arroyo." 28 Oct 1985, *Ma. Guadalupe Ayala 345* (HOLOTYPE: TEX!).

Similis *M. quinqueflorae* L. sed foliis perfoliatis, 6-8 flosculis staminatis (vice 4-5), corollis luteis (vice viridium), staminis luteis (vice atrorum), et pedunculis ultimis 10-20 mm longis (vice ca. 5 mm longis).

Annual (?) herbs to 1 m high. Stems terete, yellowish or tan, glabrous. Leaves perfoliate, those at midstem ca. 7.5 cm long, 2.5 cm wide, widest at or near the middle, glabrous beneath or nearly so, sparsely hispid above with broad-based hairs, the undersurfaces moderately glandular-punctate. Heads arranged in a diffuse terminal corymbose panicle, the ultimate peduncles 1-2 cm long, glabrous or sparsely glandular. Involucres, at flowering, ca. 1 mm high, 2 mm wide, comprised of 3-5 imbricate scarious bracts in 1 or 2 series, their apices broadly rounded. Ray florets 1 or 2, pistillate, fertile, the ligules yellow, ca. 4.0 mm long, 3 mm wide, with apices 3-lobed. Disk florets 6-8, yellow, sterile, the corollas yellow, glabrous except for a few sessile globular glands; ovaries coarsely pubescent; anthers yellow. Fruits ellipsoid in outline, glabrous with knobby surfaces, ca. 3 mm long, 2 mm wide, at maturity forming a tough case within which is tightly nestled an ovoid black achene, the surfaces finely striate.

I have described this taxon with some trepidation for it is known from only one collection; in addition, it co-occurs with typical *Milleria quinqueflora*, the latter collected by Ma. Ayala on the same day and site (*Ayala 350* [LL]) as was the type for *M. perfoliata*. The latter is readily distinguished from *M. quinqueflora* in so many ways so as to defy the simplistic explanation that it might be some monstrosity as suggested in our discussion of the anomalous *M. triflora* (*cf.* above). Indeed, the small seeds appear to be quite plump and normal, and the yellow anthers very full of seemingly fertile pollen. When collected *M. perfoliata* was apparently in full anthesis, while the *M. quinqueflora* growing with it was well past anthesis, with only a few late fruits attached to an otherwise naked capitulescence.

During January of 1997 several graduate students from TEX visited the type locality at the senior author's request. They could not locate plants of *Milleria quinqueflora* or *M. perfoliata* at the site, although an hour or more of intense scouring was spent in and about the area. Future workers should be on the lookout for *M. perfoliata* in this region. If it is a bizarre genetic form then I am amply fooled, for were it to exist as a populational unit with or removed from *M. quinqueflora* I would have no hesitancy on recognizing this as truly distinct.

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